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both these regards, while differing from each other. Cut⁶ is now the only cut mutant used for linkage determinations involving this locus.

Additional linkage data upon the crossveinless cut distance was obtained by raising nine F_2 cultures from the cross of crossveinless to cut⁶. The crossover value was found to be 6.7 on the basis of the 2,163 flies (table 3).

The locus of crossveinless is at 13.7, as calculated on the basis of the data of the three preceding tables, and on the assumptions that the locus of ruby is at 7.5 of cut at 20.0, and of vermilion at 33.0.

Description of the Crossveinless Character; Homology with Crossveinless in D. virilis.—The somatic changes produced by the crossveinless gene seem to be restricted to the entire absence of the posterior crossvein and the almost complete absence of the anterior crossvein. There is a slight trace only of the anterior crossvein, though on casual inspection it seems to extend outward from the III-longitudinal vein about half way to the IVth. However, what is seen is largely a sense-organ that is normally present near the mid-point of the anterior crossvein and that is not affected by the crossveinless mutation. Examination of crossveinless in *D. virilis* showed that the sense organ is unaffected there also, but that the crossvein is not reduced in length or thickness as much as in *D. melanogaster*. (See figures of the crossveinless mutant in Weinstein's paper preceding this.)

The similarity of the characters is paralleled by a similarity of position on the maps of the two X-chromosomes. It seems highly probable that the two mutants are homologous, though, as Weinstein's discussion brings out, this cannot yet be accepted without reservations.

IS CROSSING OVER A FUNCTION OF DISTANCE?¹

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There is a well entrenched concept of recent genetics that hereditary factors or genes may be given fairly definite loci on chromosome maps and that these maps correspond to or represent, roughly perhaps, the actual conditions in the chromosome. The basis for this attractive and suggestive view is the premise that the distance between two genes is necessarily proportional to the percentage of crossing over which these two genes show—other things being equal. If the distance which gives one per cent of crossovers is used as an arbitrary unit of measurement, then it follows that distances on the chromosome may be calculated in terms of this unit. It has seemed to me for some time that the antecedent in this hypothetical proposition contains a more or less gratuitous assumption.

We do not know that the distance which gives 1% (or $n\%$) of crossovers is a fixed unit. Stated differently, we do not know how constant the percentage of crossing over may be between two genes to which we give a fixed distance, i. e., our arbitrary unit of measurement may itself prove to be a variable. It may be possible for the distance which gives 1% of crossing over to differ in different females of the same population, or differ between stocks. In order to throw some light on these questions I began a set of experiments in 1916 in collaboration with my colleague, Dr. E. Roberts, and several students. Although a number of these experiments are still in progress, data involving the classification of over 400,000 individuals have been accumulated and some conclusions seem warranted. A more detailed account of these experiments will appear in the current numbers of the *Journal of Experimental Zoölogy*.

In observing a large number of females (*Drosophila melanogaster*) of the generalized zygotic formula $\frac{a}{A} \frac{b}{B}$, it is common to find great differences between individual females with respect to the amount of crossing over. Some of the variability may be due to sheer fluctuations of sampling, to age, and to environmental conditions, but sometimes the deviations are so wide as to arouse a suspicion that hitherto unknown causes may be effective. If this variability is due at least in part to genetic modifiers then selection should be effective, particularly if environmental fluctuations do not mask or obliterate the effects of genetic modifiers. It was with this thought in mind that I began to select for high and low crossover value. Four selection experiments were undertaken. Series A, A' and B were low selection experiments and Series C was a high selection experiment. Each series began with a single white-eyed, miniature-winged female mated to a wild, red, long male. The F_1 females were red, long double heterozygotes $\frac{w}{W} \frac{m}{M}$ and the F_1 males were white, miniature double recessives $\frac{w}{w} \frac{m}{m}$. These were mated in pairs, giving the parental classes (red long and white miniature) and the crossovers (red miniature and white long) with the usual ratio of approximately 33% crossovers—the same value used in plotting chromosome maps. The same mating was made in successive generations, always selecting as far as was possible the widest deviates to perpetuate the line of selection. At the same time, the closest possible inbreeding was maintained, the details of which are given in our longer papers. The results indicate that selection was effective in all series.

Series A was reduced to 0% in F_{10} and remained at about 0% for two more generations. Series A', derived from Series A as a side line of selection in the F_7 , began with a female showing $1 : 91 = 1.10\%$.² This line was carried for 9 generations (F_7 – F_{15}) and also bred true to about 0%. The grand total for this entire series gave $33 : 5156 = 0.64\%$ —actually

less than 1 %. There can be no doubt but that an original crossover value of about 33% has been changed by selection, at least a marked change has followed selection.

Series *B* was entirely independent in its origin from Series *A* and *A'*; and low selection was also effective, as in the case of the preceding series. Curiously enough we have not been able as yet to reduce the crossover value to zero, or approximately zero, as in the other series. Since experiments with this series form the basis of the present paper, table 1 is given to show in condensed form the progress during selection. After the F_{28} , selection was discontinued, and the stock has bred practically true to about 5 or 6% crossing over for 22 generations (i. e., through F_{50}). Table 1 gives the percentage of crossovers for every fifth generation, and also for the total offspring in each block of five successive generations.

TABLE 1
CROSSOVER VALUES FOR EVERY FIFTH GENERATION, AND FOR THE TOTALS IN EACH BLOCK OF FIVE SUCCESSIVE GENERATIONS, IN SERIES *B* (LOW SELECTION)

GENERATIONS	CROSSOVER VALUES	GENERATIONS INCLUDED	CROSSEOVERS	TOTALS	CROSSOVER VALUES
1	28.60	1-5	10517	40567	25.93
5	24.55	6-10	10344	47295	21.87
10	16.99	11-15	3687	25333	14.55
15	11.17	16-20	4869	48277	10.09
20	9.81	21-25	3386	36693	9.23
25	7.15	26-30	576	8007	7.19
30	5.62	31-35	121	2089	6.79
35	4.18	36-40	267	4571	5.84
40	6.70	41-45	750	12453	6.02
45	6.51	46-50	350	5203	6.73
50	6.98				

Series *C*, high selection, was carried for 8 generations, but we were unable to make progress in selecting upward. On the contrary, we were greatly astonished to find in the F_7 , 9 out of 72 pairs, which gave almost no crossing over at all, although they produced a large number of offspring. The remaining 63 pairs gave about the usual crossover value. The totals for these 9 paired matings were:

26 crossovers : 1055 total = 2.46% crossing over.

These same genes should have given 33% crossing over if they agreed with the usual values used in plotting chromosome maps. The natural inference is that any attempt to increase crossing over leads to double crossing over and thus to very low crossover values (practically zero). The explanation implies that these 9 females showed a marked *decrease* in crossover values, despite high selection, because they gave almost nothing but double crossovers. Series *C* was dropped, but we hope to

repeat the experiment and test out the region between white and miniature in such females.

The effects of selection on crossover values may be due to one or a number of causes, some of which suggest themselves almost immediately. The most promising and probable explanation seemed to me to be that crossing over is either due to or markedly modified by multiple factors. In order to test out this view, I crossed the low crossover stock of Series *B*, which shows 5-6% crossing over, to ordinary stock which shows 33% crossing over. Table 2 gives the results of this experiment. The first line of the table gives for comparison the frequency distribution of crossover values in an ordinary population. There were 90 females in this sample but I have eliminated two very wide deviates from the distribution, because the number of offspring on which their crossover values were based was extremely small. One of them showed $1 : 8 = 12.5\%$; and the other showed $6 : 8 = 75\%$. The population as a whole showed 30.68% crossing over and the mean female had a value of 30.55%. The average number of offspring per female and the totals show that the values for the females both individually and collectively are as reliable as can be reasonably expected. The second line of the table shows the first generation in Series *B*, which resembles closely the sample just described. After 28 generations, selection was discontinued. Thereafter the generations were perpetuated by en masse matings. In the F_{42} , I mated 50 red, long females heterozygous in white miniature $\frac{w\ m}{W\ M}$ to stock white miniature males $\frac{w\ m}{w\ m}$. All except one were fertile and the distribution of their crossover values is given as the low P_1 parent in table 2. Mating them to ordinary stock males would not change the crossover values which such low females show. We cannot know positively what the crossover value of each white miniature male parent was, but we have no reason to suppose it differs greatly from the values given for the first generation of Series *B* or the ordinary stock, both shown in table 2. We have used this same white miniature stock in class work and have always found it to give the regular "map value" of about 33%.

It was virtually impossible to breed all of the F_1 hybrid females from each pair separately. I decided to breed exhaustively 50 red long F_1 females $\frac{w\ m}{W\ M}$ to their F_1 white miniature brothers $\frac{w\ m}{w\ m}$ to obtain a sample frequency distribution of F_1 females coming from a single P_1 pair (pair No. 18). Forty-seven of these 50 females were fertile and gave an average of 465 offspring per female.³ The range of F_1 crossover values shows quite clearly that they lie between the low and the high parents. The value of the mean female and the crossover value of this total F_1 population show the same thing. One F_1 female showed a ratio of $1 : 36 = 2.77\%$, but since the ratio is based upon such a small total we need not lay much stress on this wide variate.

TABLE 2

THE DISTRIBUTION OF CROSSOVER VALUES IN NORMAL POPULATION, IN LOW CROSSOVER STOCK, AND IN HYBRIDS BETWEEN THESE

GENERATIONS	NUMBER OF VARIATES	THE DISTRIBUTION OF CROSSOVER VALUES															MEAN VARIATE	σ	CROSS- OVERS	TOTAL	% OF CROSS- OVERS	AVERAGE NUM- BER OF PRO- GENY PER VARIATE
		5.1	5.5	7.5	10.5	13.5	16.5	19.5	22.5	25.5	28.5	31.5	34.5	37.5	40.5							
Sample population.....	88	—	—	—	—	—	—	7	11	19	28	15	5	3	30.55	4.28	6465	21071	30.68	239.4		
1st generation, Series B.....	34	—	—	—	—	—	—	3.5	3	10	6	3	2	2	28.85	5.58	2056	7189	28.60	211.4		
P_1 low patent.....	49	7	26	15	1	—	—	—	—	—	—	—	—	—	5.11	2.10	425	7948	5.35	162.2		
P_1 hybrid females.....	47	1	—	2	10	16	12	6	—	—	—	—	—	—	13.88	3.64	3216	21853	14.72	465.0		
P_1 samples of each P_1	45	—	—	10	18	10	6	1	—	—	—	—	—	—	11.50	3.10	5213	39416	13.23	875.9		
P_2 from P_1 No. 2.....	33	2	1	5	8	8	5	3	1	—	—	—	—	—	12.24	4.90	1060	7812	13.57	236.7		
P_2 from P_1 No. 5.....	39	—	—	—	5	13	12	5	1	2	—	—	—	—	16.19	4.70	1477	9001	16.41	230.8		
P_2 from P_1 No. 6.....	76	—	1	3	14	23	22	6	3	3	1	—	—	—	14.96	4.39	3161	21701	14.57	285.5		
P_2 total.....	148	2	2	8	27	44	39	14	5	5	1	—	1	—	14.66	4.81	5698	38514	14.79	260.2		

In addition to the F_1 distribution coming from a single P_1 pair, I also obtained a sample crossover value of the F_1 coming from each of 44 other P_1 females. I chose at random four F_1 red, long double heterozygotes from each P_1 pair. Each group of four F_1 females was mated to white miniature F_1 brothers. Thus we secured crossover values for 45 different F_1 groups, each group coming from a single P_1 pair. These F_1 crossover values are put in the form of a frequency distribution in the fifth row of table 2. Here again we find the F_1 values intermediate between the low stock and the original population. In no case was an F_1 value as low as the mean or mode of the low parent nor as high as the mean or mode of the original population.

Three distinct and separate F_2 distributions were reared, coming from P_1 pairs No. 2, 5 and 6. The value of each original P_1 female, together with the crossover ratio of its F_1 and F_2 progeny, is given in table 3.

TABLE 3

THE DATA ON P_1 PAIRS NO. 2, 5, AND 6, FROM WHICH THE F_2 DISTRIBUTIONS WERE OBTAINED

P_1 PAIR NO.	CROSSOVER VALUE	F_1 CROSSOVER VALUE	F_2 CROSSOVER VALUE
2	21:382 = 5.50	29: 464 = 6.25	1060: 7812 = 13.57
5	7:193 = 3.63	72: 530 = 13.59	1477: 9001 = 16.41
6	6:178 = 3.37	251:1730 = 14.51	3161:21701 = 14.57

The F_2 distributions of table 2 show a wider range than the low parent or the F_1 . In fact, the total F_2 population with 148 pairs gives some females as low as the low parent and some as high as the original population. The mode is between the two stocks. It is clear that the results of these hybridization experiments bear the distinctive features of multiple factor inheritance with incomplete dominance; for the F_1 is intermediate and the F_2 is likewise intermediate in its average but the F_2 shows a conspicuous increase in range which easily overlaps both original P_1 distributions. The increase in the standard deviation of each F_2 population and of the total F_2 distribution over that of the F_1 or P_1 puts these facts in concrete terms. Therefore, we can hardly escape the conclusion that multiple factors have a striking influence upon crossover values. In the frequency distributions of table 2, some variates will necessarily have little meaning because their crossover values are based upon small totals. I have thought it desirable to include every variate and thus withhold no data rather than include only such females as produced more than a fixed minimum of offspring. However, in order to show that the extremes in the F_2 population are segregates, rather than fluctuations of sampling, I have given in table 4, detailed data on the highest and lowest 12 variates in the total F_2 frequency distribution of table 2. The lowest 12 variates have values from 0%-9% and cover about the same range as the low

parent; while the highest 12 have values above 21% and cover about the same range as the high parent. The values for both low and high F_2 variates are based upon totals which are just as satisfactory as any in the population, where the average number of progeny per female was 260. The total F_1 included 61,000 offspring and the total F_2 distribution is based upon 38,500 offspring.

TABLE 4

THE HIGH AND LOW VARIATES OF THE TOTAL F_2 DISTRIBUTION IN TABLE 2

LOW VARIATES			HIGH VARIATES		
RECORD NUMBER	CROSS- OVERS	TOTAL = CROSSOVER VALUE	RECORD NUMBER	CROSS- OVERS	TOTAL = CROSSOVER VALUE
2- 2	1	: 35 = 2.86	2-32	66	: 287 = 23.00
2- 6	18	: 216 = 8.33	5-21	52	: 154 = 33.77
2-19	14	: 223 = 6.28	5-22	45	: 178 = 25.28
2-22	0	: 19 = 0.00	5-24	69	: 325 = 21.23
2-25	8	: 168 = 4.76	5-28	112	: 466 = 24.03
2-28	14	: 174 = 8.05	6-10	107	: 416 = 25.72
2-33	22	: 329 = 6.69	6-21	56	: 241 = 23.24
2-34	25	: 280 = 8.93	6-23	71	: 287 = 24.74
6- 8	11	: 281 = 3.91	6-24	61	: 251 = 24.30
6- 1a	32	: 394 = 8.12	6-11a	33	: 145 = 22.76
6- 2a	23	: 275 = 8.36	6-13a	26	: 89 = 29.21
6-35a	20	: 272 = 7.35	6-16a	62	: 295 = 21.02
Total.....	188	: 2666 = 7.05	Total.....	760	: 3134 = 24.25

In obtaining a crossover value for any two genes like white and miniature we find much variability among the females which serve to make up the general population from which our map value is derived. This variability is due to numerous modifying factors. Selection has evidently sifted out certain relatively pure combinations of these modifiers, hence the low variability of our low crossover stock. The hybridization experiments indicate that the amount of crossing over is at least markedly influenced if indeed it is not actually determined by multiple factors. There are several ways in which multiple factors might possibly change the crossover value which two genes show. In modifying the crossover value of white and miniature from 33% to 6% or to 0% we might suppose that we had either moved the locus of genes or that we had eliminated the usual single chromosomal twist between these two genes. Since the allelomorphic relationships between red and white and between long and miniature have not been disturbed when we mate low crossover stock to the original population, the latter alternative explanation seems preferable. We can evidently change by selection the amount of twisting which members of an homologous pair of chromosomes show. Now, if the difference between practically no crossing over (Series *A* and *A'*) or between 6% crossing over (Series *B*) and normal crossing over (33%) is due to multiple

factors, we then naturally wonder just what part "distance between two genes" on a chromosome map may play in determining linkage values. Our current view is that "the percentage of cases in which two linked genes separate (amount of crossing over between them) is necessarily proportional to the distance between these genes,—other things being equal," i. e., under ordinary circumstances and in the absence of unusual factors or environmental conditions which geneticists recognize. But evidently under ordinary circumstances, the percentage of crossing over is a variable which is determined by the different possible combinations of multiple modifying factors; hence the percentage of crossing over cannot be proportional to the distance if the distance remain constant. For example in Series *B* we find 6% crossing over, and so we should conclude that the distance is less than one-fifth of what it originally was before we began selection. To maintain our original position, we must conclude that the percentage of crossing over and the distance are correlated variables, if the proportion is to remain reasonably constant. The dilemma will hardly aid us in determining what had happened to almost all of the distance and the genes between 0 and 33 in Series *A* and *A'*, where crossing over was practically eliminated. In view of these considerations it would perhaps be simpler to conclude that linkage is not a function of distance, i. e., crossing over is not necessarily proportional to distance. The distance between two genes may remain fairly constant, but the amount of crossing over depends upon numerous hereditary factors.

¹ Paper No. 14 from the Laboratory of Genetics, Illinois Agricultural Experiment Station.

² In giving crossover values, I shall put the data in the following form throughout this paper:—crossovers: total = per cent of crossing over. Since the classes are always the same, repetition can be avoided.

³ I am indebted to Dr. E. Roberts and Mr. P. M. Woodworth for carrying this generation in part.

INTERSPECIFIC HYBRIDS IN *CREPIS*

I. *Crepis capillaris* (L.) Wallr. \times *C. tectorum* L.

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Interspecific hybrids, particularly those having different specific chromosome numbers, have in the past figured conspicuously in establishing the now generally accepted principle of the individuality and continuity of the chromosomes. It is probable, therefore, that a study of the hereditary characters of species hybrids may give further information concerning the chromosomes as the carriers of the determiners of hereditary characters